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Vegetative reproduction in the New England *Frullaniae*

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Very little emphasis has as yet been laid upon the occurrence of adventive branches, or propagula, in the genus *Frullania*, perhaps for the reason that such propagula, at least in the New England species examined by the writer, offer no taxonomic distinctions, as do the gemmae in *Metzgeria*. In any case, but few references to such propagula can be found in the previous literature.

Dr. Evans ('97), in his monograph on the North American *Frullaniae*, while he makes no reference to such propagula in his introductory remarks, describes the upright flagellate branches of *F. Bolanderi* Aust. but does not ascribe to them any characters of vegetative reproduction. In comparing this species with *F. eboracensis* Gottsche, he says: "*F. eboracensis* occasionally produces flagella-like branches, but they are always leafy, and are a rather unusual feature of the plant"; and in the description of *F. eboracensis*, "sometimes flagelliferous."

However, in his *Hepaticae of Puerto Rico* ('02-) he describes a variety of adventive branches, propagula and gemmae, arising from different situations upon the plant. Of these, the propagula arising from the modified leaves of *Rectolejeunea flagelliformis* Evans and *Cheilolejeunea decidua* (Spruce) Evans bear the most resemblance to those of the species of *Frullania* which are discussed below.

While a sharp distinction can hardly be made between gemmae and adventive branches or propagula, a gemma, as a rule, grows to a specific size while still united to the parent plant and germinates after being shed. An adventive branch, on the other hand, whether arising from a "Brutblatt" or from some other position upon the plant, begins as an irregular mass of cells and may develop a branch with several leaves before becoming detached.

Berggren ('65) describes in careful detail the propagula upon

the leaves and lobules of *Frullania fragilifolia* Tayl. and figures three lobules with shoots of different ages. Schostakowitsch ('94) treats of the adventive branches of *F. dilatata* (L.) Dum. and *Porella platyphylla* together, figuring a "Vorkeim" of *Porella* which greatly resembles that of our Frullaniae.

Pearson ('02) and Macvicar ('10) refer to the remarkable caducous leaves of *Frullania fragilifolia* but had not observed them to be Brutblätter, although they mention the shoots on the lobules.

Cavers ('03) describes the vegetative reproduction in two European species of *Frullania*. In *F. fragilifolia* Tayl. the easily detached hooded lobules give rise to leafy shoots from their marginal cells. In *F. dilatata* (L.) Dum. "the outer surface of the perianth in this species bears numerous irregular outgrowths, each made up of from two to five or six cells. These outgrowths may be regarded as gemmae." Warnstorf ('03) describes these structures in *F. dilatata* in somewhat more detail, as well as small thin-walled Keimkörner upon the leaves of ♂ plants, and suggests that these two types of gemmae may serve to reproduce the ♀ and ♂ plants respectively.

Hans Buch ('11) merely refers to the Brutblätter of *F. fragilifolia* without any further description.

Of the eleven species of *Frullania* at present reported from New England, seven belong to the subgenus *Trachycolea*, one to *Homotropantha*, two to *Thyopsiella*, and one to *Diastoloba*.

Upon examination, adventive branches were found in three of the species of subgenus *Trachycolea*, viz., *F. eboracensis* Gottsche, *F. Brittoniae* Evans, and *F. riparia* Hampe; as well as in *F. plana* Sull., the representative of subgenus *Homotropantha*. Some scanty material of *F. inflata* Gottsche and *F. saxicola* Aust. was examined fruitlessly, but adventive branches could probably be demonstrated with a larger supply of material.

In the subgenus *Thyopsiella*, material of *F. Asagrayana* Mont. from four different states was examined, with no traces of Brutblätter. *F. Tamarisci* (L.) Dum., both Nova Scotian and Swiss material, gave similar negative results. The same was true of the only *Diastoloba*, *F. Selwyniana* Pearson from Maine.

F. eboracensis Gottsche easily leads all the New England species

in regard to the abundance and luxuriance of its means of vegetative reproduction. As the adventive branches upon all species examined precisely resemble one another, only *F. eboracensis* will be considered in detail and figured. Material was examined from four states, and the Brutblätter were by far the most common upon the Connecticut plants, being observed but once each upon plants from Maine and from Waterville, N. H. These observations and figures have been almost entirely taken from material growing upon *Juniperus* in the vicinity of Dr. Hooker's Cabin, at Farmington, Conn.

Branches with deciduous leaves are frequently produced upon both ♀ and ♂ plants. These may be considered as Brutblätter, as their method of separation is schizolytic, leaving behind one row of cells and the stylus. If a branch is moistened and handled with extreme care, the Brutblätter can be seen in position, but they are excessively fragile.

Whether or not the production of Brutblätter is induced by drought, the cause has evidently no connection with the time of year, as plants collected in January and May from neighboring stations bore equally good Brutblätter. While Brutblätter are equally common upon ♀ and ♂ plants, the writer has not yet observed any upon plants with mature capsules, although thick-walled cells are occasional upon perichaetial bracts as well as upon underleaves. Neither were they observed upon perigonal bracts.

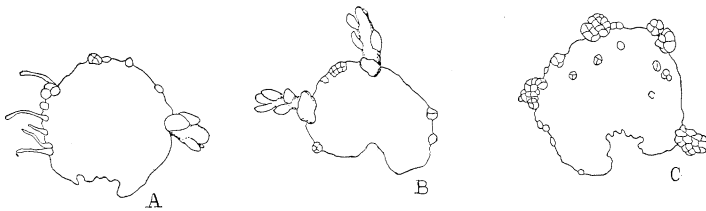


FIGURE 1. *Frullania eboracensis*. A, leaf with rhizoids, $\times 40$. B, leaf with two shoots, $\times 40$. C, leaf with seventeen cell masses, $\times 40$.

The leaves themselves often develop rhizoids, by the projection and lengthening of marginal cells, thus being prepared to get a foothold wherever the leaves happen to be shed. (FIG. 1, A.)

The gemmalike masses of cells are developed from the margin

or from the row or two of cells just within. A single favorable leaf may have eight or ten marginal cells in various stages of division, making quite a border, besides one or two entire shoots with more or less developed leaves. (FIG. 1, *B*.) The largest number of cell masses counted by the writer upon any one leaf is seventeen, but these were not all marginal. (FIG. 1, *C*.)

A marginal cell first becomes more or less pigmented with red-brown, or rather, with burnt sienna mixed with a very little carmin lake and just a touch of black, so that it is strikingly contrasted with the clear green of the rest of the leaf; or if upon red ♂ plants, the color becomes still deeper and richer. The cell wall thickens, and the cell expands and projects beyond the margin to some extent. (FIG. 2, *A*.) It first divides by a wall perpendicular to the margin, making two approximately hemispherical cells. These divide next in a plane about in line with the margin, but this is not a continuous line, so that the four resulting cells are

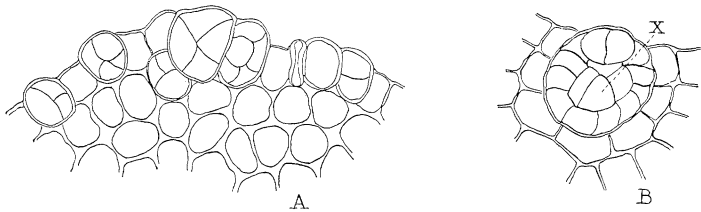


FIGURE 2. *A*, margin of leaf with cells in various stages of division: note the cell that has been compressed by its neighbors; $\times 250$. *B*, further developed cell mass, showing triangular apical cell in center, $\times 250$.

not all of quite the same size. They in turn divide in a plane about parallel to the leaf surface. One of the outer cells cuts out a three-sided pyramidal apical cell (FIG. 2, *B*), and the leafy shoot arises directly from this, without having first become detached from the leaf and while the leaf is still growing upon the plant.

The lobules bear, with equal frequency, cell masses and shoots either upon the top of the hood or about its mouth. (FIG. 3, *A*, *B*.) A few hoods had shoots so well developed that several of the upper leaves had hoods of their own. (FIG. 3, *C*.)

The first leaves on the shoots are mere rudiments, but succeeding leaves are increasingly developed, and underleaves soon

appear. (FIG. 3, *D*). The largest shoots have quite the aspect of normal branches. (FIG. 3, *E*.)

On some fresh material from Farmington, growing on young elm trees in a bog, the cell structure of the leaves differed in being thinner-walled, with less conspicuous trigones and almost no intermediate thickenings. This condition approaches that of *F. Boleri* Aust. of the Pacific coast, which besides its characteristic upright flagellate shoots has Brutblätter exactly like those first described for *F. eboracensis*.

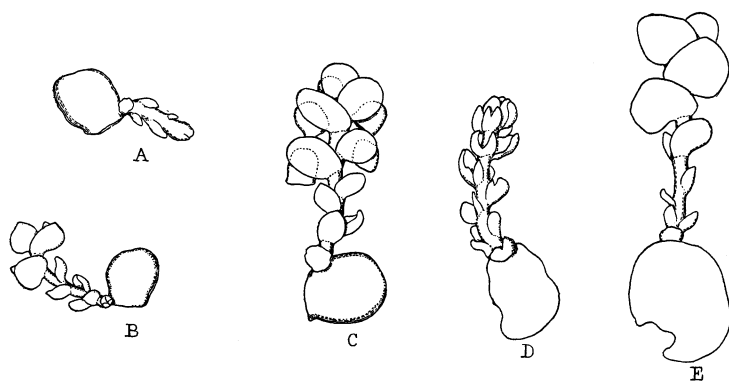


FIGURE 3. A-C, hoods with shoots in different stages; D, E, leaves with well developed shoots.

In *F. riparia* Hampe from North Pownal, Vermont, the Bruchblätter were not caducous, and the cell masses as a rule were not marginal but arose from cells about two rows back from the margin.

F. Brittoniae Evans, which is very close to the European *F. dilatata*, in some material from Waterville, N. H., bore cell masses and shoots upon leaves likewise not caducous.

The adventive branches in *F. plana* Sull. are borne, not upon the oldest and more or less dirt-encrusted portions of the plant, but upon the growth of the past season. These leaves also were not caducous, neither did they produce rhizoids. The adventive branches closely resemble those of *F. eboracensis*, except that they are of a rather dark green instead of being pigmented with red-brown.

According to these observations, the production of Brutblätter

is more frequent in the dioicous rather than in the autoicous species of *Frullania*. *F. eboracensis*, *F. Brittoniae*, and *F. riparia* are all dioicous, as is *F. Bolanderi*; while *F. plana*, although autoicous, is usually sterile. All the European species of *Frullania*, with the exception of the recently described *F. cleistostoma* Schiffner & Wollny, are dioicous.

The writer would express her thanks to Dr. A. W. Evans for his kind assistance; and would be glad to examine any further propagula-bearing material of *Frullania*, other than *F. eboracensis*.

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